Scent marking strategies in mammals *

by

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With 28 figures

INTRODUCTION

1. *Social Odours*

Mammals are complex creatures and often they live complicated social lives in which order is maintained by the transmission of information between individuals. Sometimes the signals are passed by sound, sometimes visually, and very often by odour. It is this latter modality, olfactory communication, that forms the subject of this paper.

In order to introduce the topic, and to make the point that the subject has long been of interest to man, I would like to bring to your attention the oldest scientific reference with which I am familiar. The work in question is concerned with the Pleistocene Mammoth and is lodged in France, not in some library, but in the Lascaux caves. There, a stone-age natural historian and accomplished artist has faithfully depicted, in full flow, the temporal scent gland of this long extinct creature (Fig. 1). The same phenomenon can still be seen today, in the two living species of elephants.

Olfactory communication has a number of advantages over other forms of signalling. It can be used when visual or auditory signals are difficult to detect, for example in the dark, underground, or in thick vegetation. In addition, odours can be deposited in the environment as scent marks and then they provide a spatial and historical record of an individual's movements and behaviour. As signals, scent marks have the very important property of remaining active for long periods of time, even in the absence of their author.

The odours used as signals by mammals are not equivalent to the pheromones of lower animals; they are usually complex mixtures, rather than simple chemicals, and responses to them are not stereotyped but instead depend upon context and prior experience. BROWN (1979) has suggested, therefore, that the term "social odour" would be more appropriate for mammalian chemical signals. Mammals are often profligate in their use of social odours; they are equipped with a quite dazzling array of odoriferous
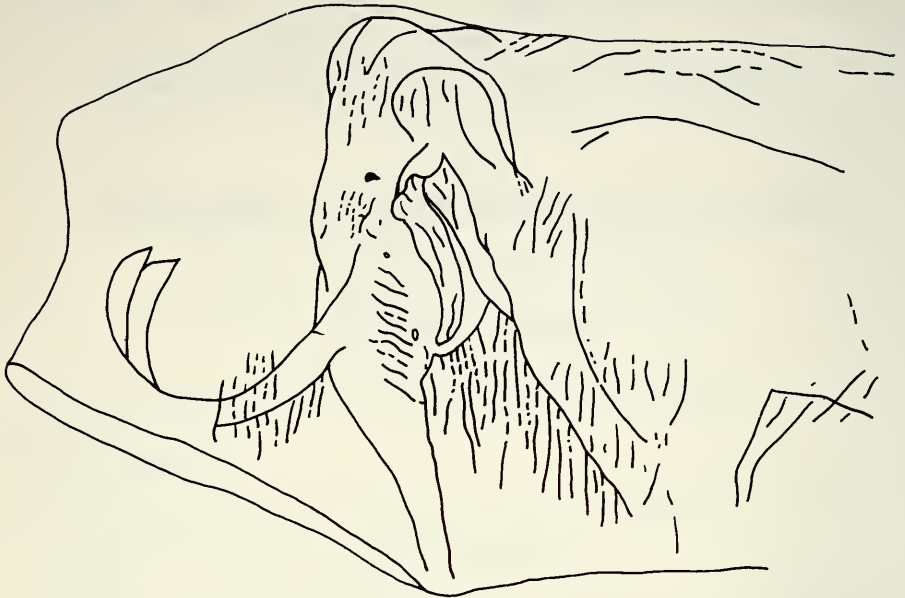
Figure 1.

Drawing, based on a cave painting, of a Mammoth showing the discharge of the temporal scent gland.

Figure 2.

European badger *Meles meles* scent marking with its sub-caudal scent organ. (Photograph by courtesy of Hans Kruuk. From GORMAN, KRUUK & LEITCH 1984).

skin glands and they make full use of the splendid olfactory opportunities that are presented by their urine and faeces. Olfactory communication is a broad topic but here I shall restrict myself to just one aspect of the subject, that of territorial scent marking (Fig. 2). Let me start by setting the scene with an account of the probable function of such behaviour (GOSLING 1982, GORMAN 1984).

2. *The function of territorial scent-marking*

Individual animals can gain an advantage over others by denying them access to resources such as food and mates. One way to do so is by being territorial, and excluding other individuals from a particular area of ground. Scent marking is centrally involved in the advertisement of land tenure in such territorial societies. Although territories are vigorously defended when the occasion demands, fights over the possession of a territory are, in fact, quite rare. This is because individuals recognise occupied areas and are generally reluctant to enter them. On those occasions when a conflict does develop between a resident and an intruder it is usually settled in a conventional manner, with the intruder withdrawing without escalation to serious fighting (Fig. 3).
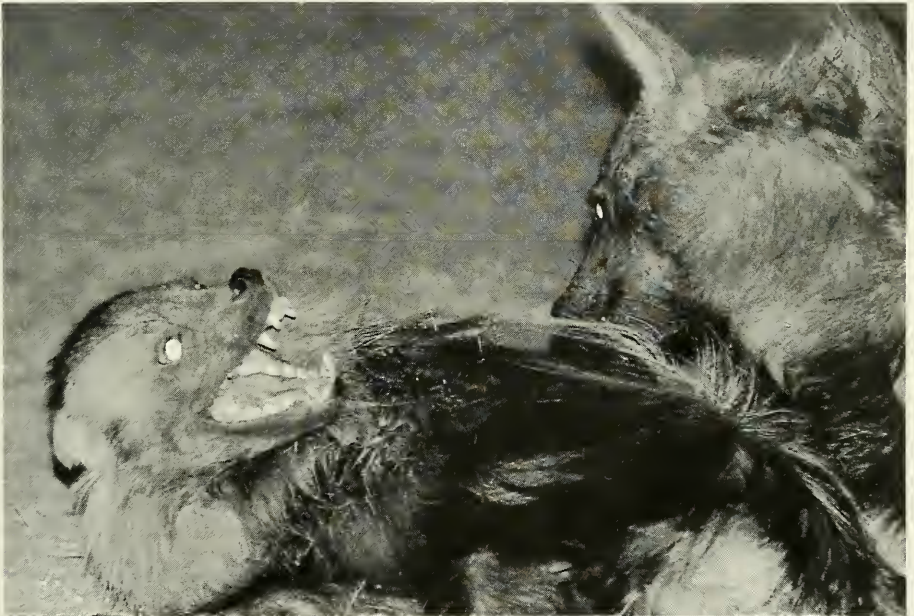

FIGURE 3.

A ritual fight between two brown hyaenas. The territorial owner is on the right, the intruder on the left.

Animal conflicts are settled by convention, rather than by fighting, when there is a clear asymmetry between the two individuals. The asymmetry may involve an obvious difference in body size, and hence in potential fighting ability, or it may be more subtle and

couched in terms of how much each of the two potential combatants stands to gain or lose from the conflict. This will, of course, determine the likelihood of each individual escalating the conflict to a bloody battle.

The individual, or individuals, resident in a territory have more to gain from retaining the territory than do intruders from taking it over, and will, therefore, be more likely to escalate an encounter than will an intruder. This is because residents will have invested a great deal of energy and time into getting to know their areas and resources, and may well have dependent young. In addition, a resident, by virtue of having gained and held a territory, is likely to be an individual of high quality and fighting ability. Since escalation brings the risk of injury and death to both animals, it is in the resident's interest to allow itself to be recognised as such, in a completely unambiguous manner and in a way that precludes any possibility of cheating or bluff. Territorial scent marking may be one way to do so; only a long-term resident can have had the opportunity to pepper an area with scent marks. Consequently, if an intruder should meet an individual whose odour *m a t c h e s* that of the majority of scent marks in the area, then it can be reasonably sure that it has met the resident. Having identified the resident, by definition a quality
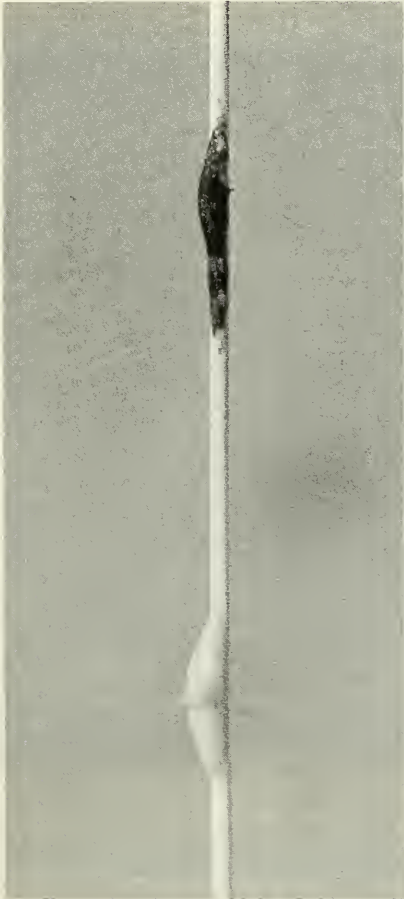

FIGURE 4.

A grass stalk marked with paste by a brown hyaena.

individual quite likely to rapidly escalate the conflict to horrible heights, the intruder would do well to withdraw as rapidly as possible. In essence, the scent marks in a territory act as a cue to potential fighting ability and to willingness to fight in an asymmetric contest between resident and intruder.

3. The deployment of scent-marks

We now come to the central problem facing all animals that scent mark their territories; where is the best place to put the scent marks? Social odours are a limited resource whether the animal be using faeces, urine or the secretions of skin glands. Scent marking can also involve a significant investment in terms of time and energy. For example, the brown hyaena *Hyaena brunnea* produces a scent mark which is 97% lipid (Fig. 4). Over the course of a year an adult hyaena will deposit around 30,000 of these marks, the equivalent of about 40% of its own body weight! This is clearly a significant investment, particularly so for an animal that lives in the barren and desolate Namib and Kalahari deserts.

Given such costs of time and energy, one would predict that scent marks will not be deployed at random but instead at c o n s p i c u o u s   l a n d m a r k s and in an o r g a n i s e d   p a t t e r n that maximises their chance of being discovered by the individuals to whom they are directed. This is the major question that I wish to address in this paper. In doing so I shall describe how we have gone about the task of mapping patterns of scent marking in three very different types of mammals; the hyaenas, the European mole *Talpa europaea* and the European otter *Lutra lutra*. These studies have been carried out in collaboration with Dr. Gus Mills, Dr. David Stone and Dr. Beverley Trowbridge respectively. These animals are of very different sizes and mobility and gathering data from each them has necessitated the use of quite different field techniques.

Intuitively, one might imagine that the best place to deposit scent marks would be along the borders of a territory so as to give the earliest possible warning to a potential trespasser. As we shall now see, the situation is much more complex than that.

HYAENAS

All four extant species of hyaenas scent mark their territories by drawing grass stems through their anal pouches to leave on them a deposit of long lasting secretion or "paste" (Figs 4 & 5). In addition, although they may defaecate anywhere within the territory, on occasion they do so at specific latrines where faeces may accumulate in large numbers, sometimes over a period of many years. Both types of scent marking are involved in the advertisement of territorial ownership.

Hyaenas appear to adopt one of two distinct strategies in terms of how they distribute scent marks in their territories. The first approach to the problem is exemplified by the population of spotted hyaenas *Crocuta crocuta* living in the Ngorongoro crater in East Africa (Fig. 6, KRUUK 1972). In this food-rich area the hyaenas live in large and stable social groups, or clans, each containing up to 80 individuals, and each occupying a relatively small, 30 km², group territory. In these territories, the latrines and pasting places are found on, or near, the borders and are replenished during regular border patrols (Fig. 7). The hyaenas visit the latrines en masse, and after sniffing and scratching, they add their own contribution to the pastings and to the piles of stinking and visually striking white ordure.

FIGURE 5.

Brown hyaena scent marking a grass stem with its sub-caudal pouch.
(Photograph courtesy of Gus Mills).

A quite differrent strategy of territorial demarcation is shown by brown hyaenas living in the much less productive Kalahari desert in Southern Africa. There, the hyaenas live in small groups of 5-10 individuals, but they defend large group territories in excess of 500 km². Our own data on scent marking were collected in the Kalahari Gemsbok national Park, an area of semi-desert covered with sand-dunes broken by pans and by the dry bed of the river Nossob. The dunes and river bed form distinct habitats with the latter providing a much higher density of potential food. Between 1976 and 1978 we studied 2 females and 3 males who formed part of the Kwang clan (MILLS, GORMAN & MILLS 1980). These hyaenas, which were fitted with radio-collars, were located at dusk and followed in a vehicle, with the aid of a spotlight. Each time a hyaena stopped to paste, or to visit a latrine, its position was noted on a large scale map of the area. In total we followed the hyaenas for 1947 km and recorded the positions of 5144 pastings (Fig. 8) and 169 latrines. This data set is a representative sample of the places within the territory where hyaenas deposited scent marks. We can assume that the marks present at any given instant of time will be dispersed in an essentially similar way. The *a c t u a l   n u m b e r* of scent marks that are present in a territory at any given point in time will be a function of the rate at which new marks are laid down and of the rate at which old ones decay. In the Kwang territory there were five to seven adult animals each travelling, on average, 30-40 km/night and pasting at a rate of 2.64 marks/km. We do not have an accurate measurement of how long a paste mark remains active but it can be detected by the human

FIGURE 6.

The organisation of the group territories of spotted hyaenas in the Ngorongoro crater. (After KRUUK 1972).

nose for at least 30 days, and probably for much longer by a hyaena. Taking 30 days as a conservative estimate of the average lifespan of a pasting means that the Kwang territory would contain, at any given time, upwards of 20,000 active pastings, some four times the number shown in Figure 8.

It is clear from Figure 8 that pastings are spread throughout the whole of the Kwang territory, but not uniformly so. As a first step in describing the dispersion pattern of the scent marks we subjected them to a nearest neighbour analysis and compared the result to the distribution to be expected if the same number of pastings were randomly dispersed.
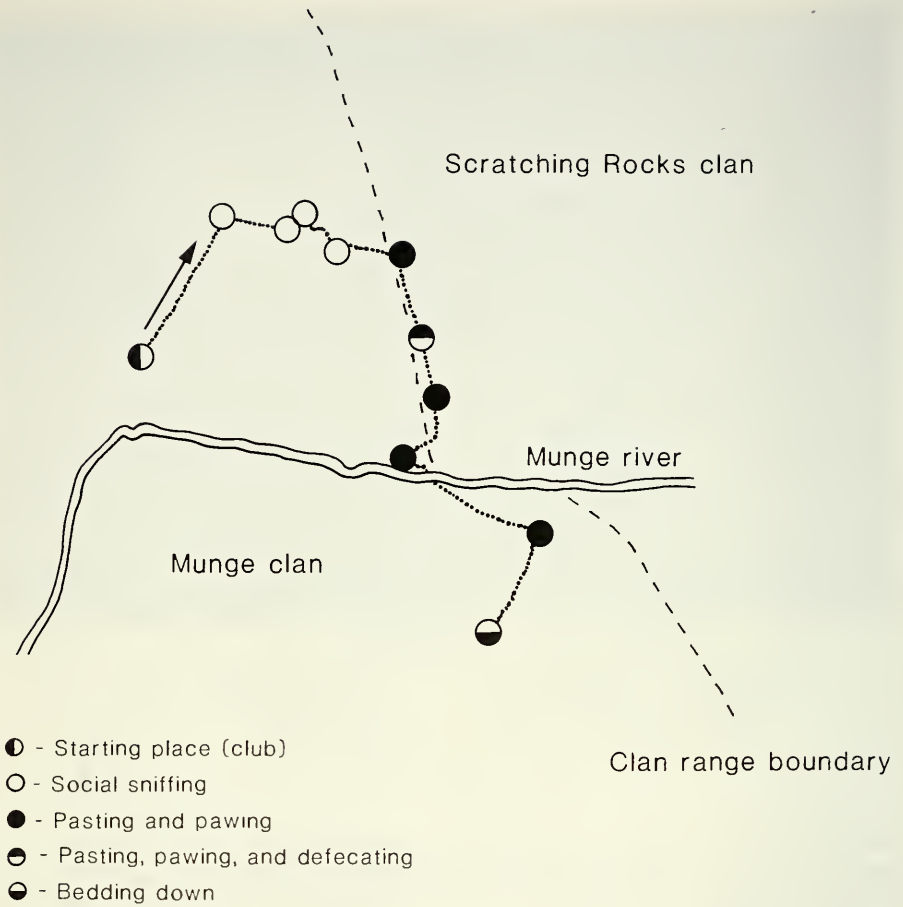
FIGURE 7.

The course taken by a clan of spotted hyaenas when pasting along their territorial border.
(After KRUUK, 1972).

The analysis showed that the two distributions were significantly different (Chisquare = 419; $p < 0.001$), with the pastings being more regularly spaced than random. The spatial pattern of the pasting sites was further analysed by means of the computer program SURFACE II which displays, graphically, spatially distributed quantitative data as a three dimensional map in which the vertical dimension reflects the value of the quantitative data, in this case the density of pasting points. To facilitate such an analysis we superimposed on the map of the Kwang area a matrix of 2.5×2.5 km squares and then counted the number of pasting sites in each. The resultant map is plotted as if seen from
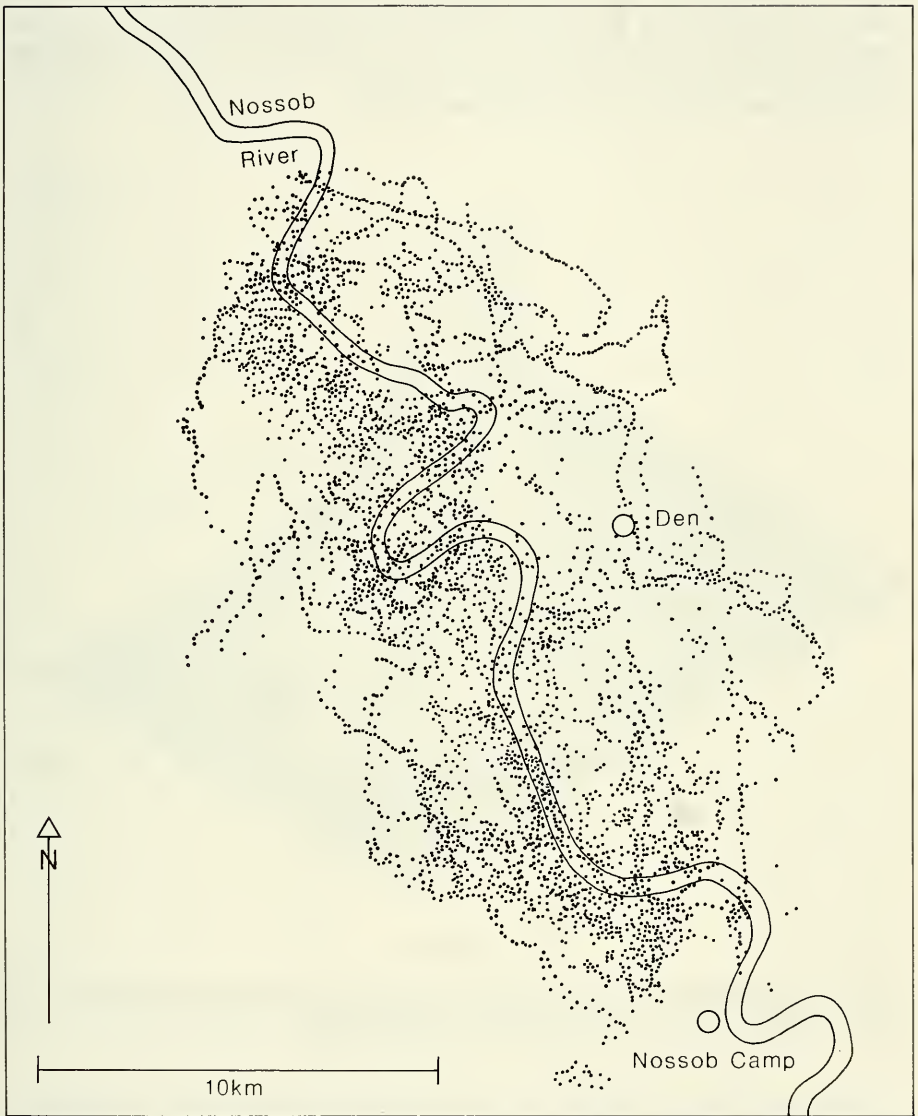
FIGURE 8.

A Map of the locations at which members of the Kwang group of brown hyaenas were seen to paste mark. (After GORMAN & MILLS 1984).

the southeast at an altitude of 35° above the horizontal (Fig. 9). The analysis shows very clearly that although paste marks were found throughout the territory, the highest densities were near to the centre, along the course of the river Nossob where the food was concentrated and where the hyaenas spent most of their time, with a progressive decrease towards the borders. It must be stressed that while the map gives a clear representation of relative differences in scent mark density throughout the territory, in reality the absolute densities were probably several times higher.
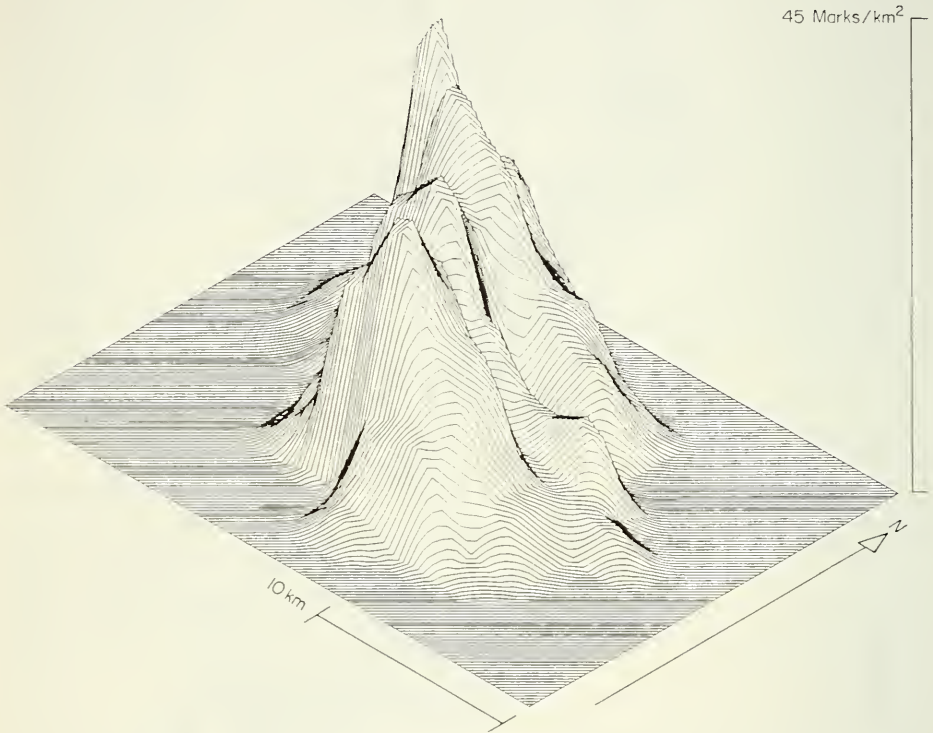

FIGURE 9.

A three dimensional map of the density of pastings in the Kwang group territory.
(After GORMAN & MILLS 1984).

I wish now to turn to efficiency of this hinterland marking strategy, to address the problem of how likely it is that hyaenas will encounter paste marks as they move into, or through, an occupied territory given this density and dispersion of scent marks. We have approached this problem by means of computer simulations in which a "hyaena" was placed at 500,000 random points on a representation of the Kwang territory and at each point its distance from the nearest pasting site was measured. The computer program SURFACE II was then used to calculate contours of equal value from the resultant set of hyaena/pasting distances (Fig. 10). The analysis shows that, even at the very edge of
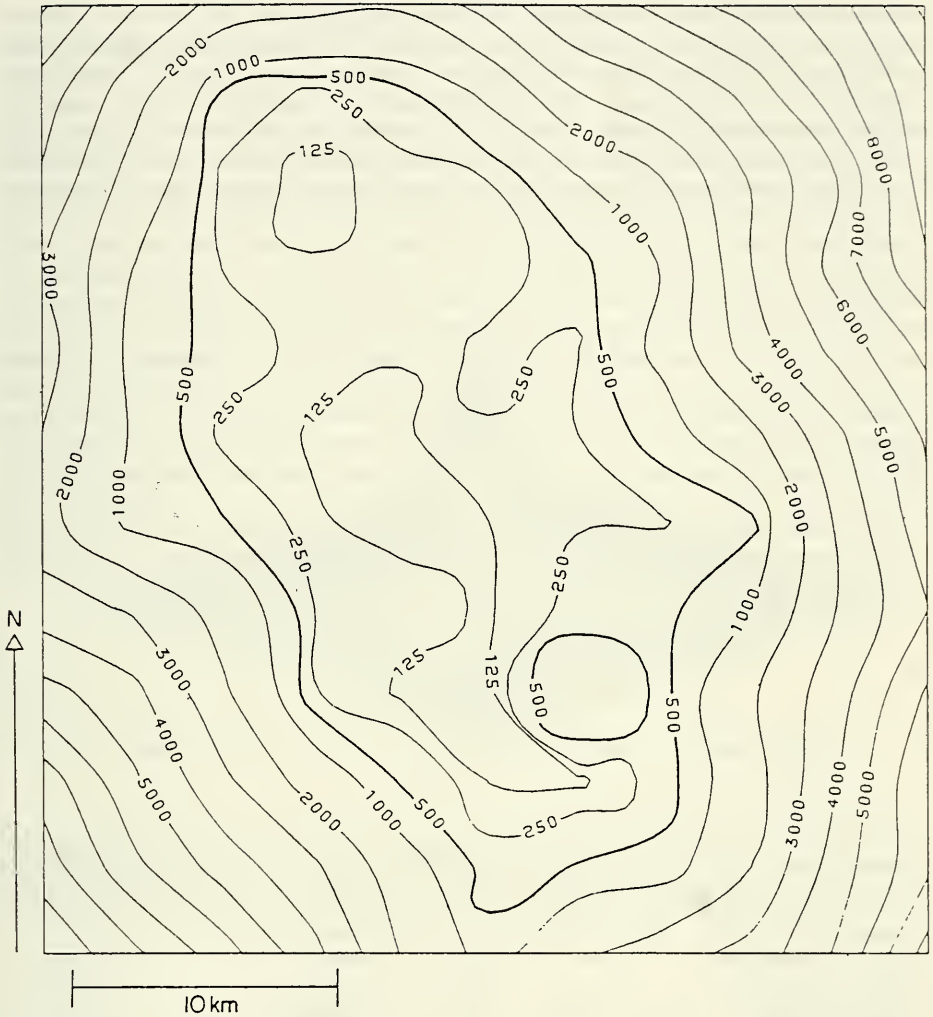
FIGURE 10.

A contour map of the average distance (in metres) between a randomly positioned brown hyaena and the nearest scent mark belonging to the Kwang group. The 500 m contour approximates to the territory boundary and contains 99% of the Kwang scent mark locations.
(After GORMAN & MILLS 1984).

the territory, a hyaena will on average be within 500 m of a scent mark and over most of the territory it will be within 250 m, a very short distance for an animal that can detect carrion from 2 km away. In the real world, where the density of scent marks is four or five times higher, these distances will be even shorter.

These then are the two strategies shown by hyaenas, the border marking of spotted hyaenas and the hinterland marking of brown hyaenas. If scent marking is indeed adaptive

then one would expect such marked differences in behaviour to have a functional significance. What is that significance? One possibility is that they are genetically determined species differences. We believe that they are not, but that instead they are adaptive responses to local conditions. Border marking gives the earliest possible warning of trespass to intruders. However, this approach involves but a single line of scent marks which must be maintained intact and replenished on a regular basis if it is to serve its function. This is possible when the supply of scent is large as compared to the length of perimeter to be marked. This is the case in the Ngorongoro spotted hyaenas where large groups share small territories and where the length of border to be marked by each individual is relatively small (Table 1). Brown hyaenas living in the Kalahari have to maintain much larger territories in order to feed themselves. Given a limited time budget, and a finite supply of scent, as territory size increases it becomes progressively more and more difficult to visit and mark the border with the regularity that is necessary to maintain an unbroken line of scent marks. The average length of border to be marked by each Kalahari brown hyaena is an order of magnitude greater than that for a Ngorongoro spotted hyaena (Table 1). In such a situation, where small clans are faced with the uphill battle of patrolling and scent-marking a very long border, hinterland marking is the safer strategy; an intruder may penetrate some distance but sooner or later it will encounter the warning signs. The important parameter in determining which strategy to follow, border or hinterland marking, appears to be the length of perimeter to be marked by each group member.

TABLE 1

Scent marking patterns in hyaenas (after GORMAN & MILLS, 1984)

Species, Locality	Group Size	Territory Size (km²)	Marking Strategy	Circumference/ Individual (km)
Aardwolf, Serengeti	1-2	1.5	Border	1.7-3.4
Spotted, Ngorongoro	30-80	30	Border	0.24-0.63
Striped, Serengeti	1	40-70	Hinterland	22-30
Brown, Kalahari	1-9	235-500	Hinterland	11-16
Spotted, Kalahari	3-15	c. 1000	Hinterland	7.5-37.0

If our interpretation of the adaptive significance of the two scent marking strategies is correct, then we would predict that spotted hyaenas living in small clans, in large territories with low densities of food, would opt for the hinterland pattern of marking.

Luckily, spotted hyaenas living in the Southern Kalahari live in small clans of 3-13 adults and occupy huge territories of over 1000 km² and can be used to test the prediction (MILLS & GORMAN 1987). We have collected scent marking data by following the 8-13 strong Kousant clan as they moved through their 1600 km² territory. In total the animals were followed for over 3500 km and the positions of 1010 pasting sites and 121 latrines were mapped. We estimate, on the basis of known distances moved and rates

of marking, that the standing crop of active marks at any given time is in the order of 1200 pastings, a much lower figure than the 20,000 estimated for brown hyaenas in the same area.

Like the brown hyaenas, the spotted hyaenas spent most of their time near to the centre of their territory, around the river Nossob, where food density was at its highest (Fig. 11). Figure 12 shows the positions of all the scent-marking sites that we saw the hyaenas use; these consisted of latrines, where the hyaenas defaecated and/or pasted and
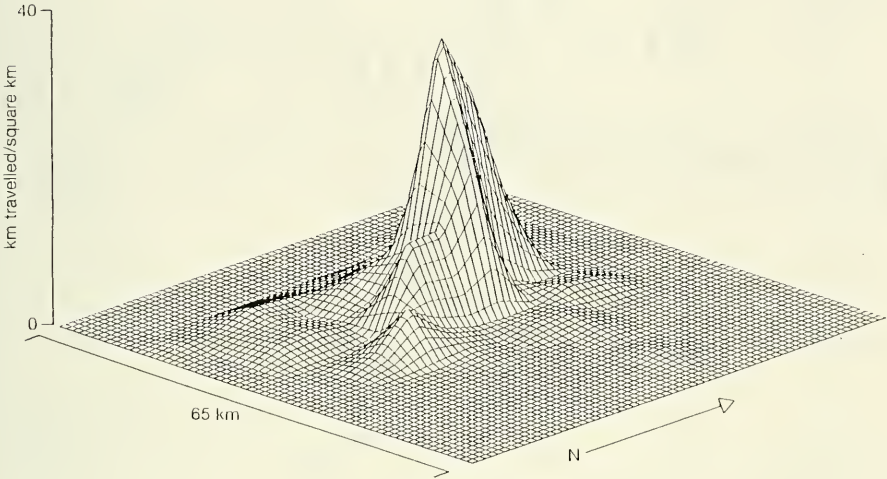
FIGURE 11.

A three dimensional map of the distances moved by spotted hyaenas, belonging to the Kousant clan, in different parts of their territory in the Kalahari. The map was prepared directly from the matrix of distances moved in 6.5 sq km map squares, and is presented as viewed from the south-east with the observation point situated 10,000 map units from the centre of the matrix and 20° above the horizontal. (After MILLS & GORMAN 1987).

pastings sites, places at which only pastings were deposited. It is clear from the map that both the latrines and the pasting sites were scattered throughout the territory, but not uniformly so. Nearest neighbour analyses of the latrines, and of the individual pastings (not pasting sites) showed that both were significantly more clumped than random (Figs 13 & 14). An inspection of Figure 12 will show that the latrines and other pasting sites were distributed in rather different patterns. The sites that received only pastings were generally dispersed throughout the territory whereas the latrines tended to be concentrated along the dry river Nossob and towards the northern and southern borders of the territory, where they crossed the Nossob, areas of intense interest to hyaenas.

The vast majority of the pastings that we saw hyaenas deposit were placed either at latrines (62%) or at some other visually conspicuous feature in the environment (Fig. 15). The latrines themselves were also associated with obvious landmarks, with only 11% in open, featureless country.
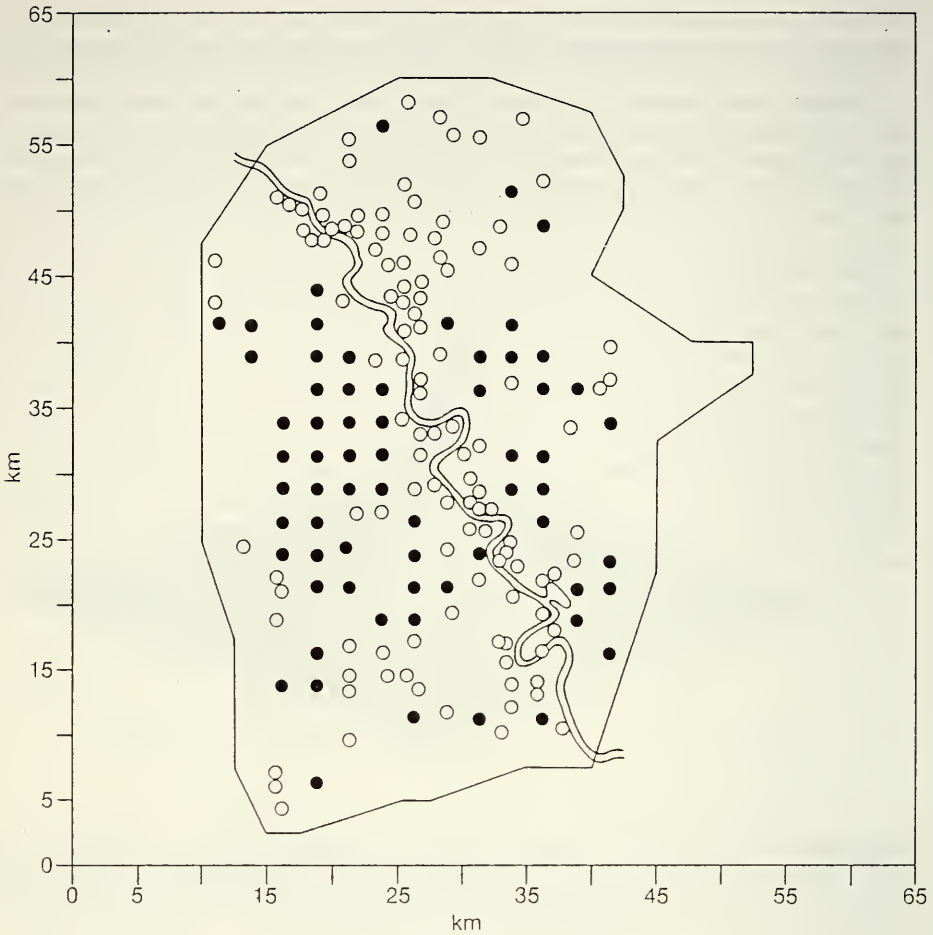
FIGURE 12.

Map of the Kousant territory showing the positions of latrines (open circles) and other pasting sites (filled circles). The continuous line shows the territory border as a restricted polygon. (After MILLS & GORMAN 1987).

Spatial differences in the density of pastings throughout the territory are shown in Figure 16. Clearly, the highest densities of pastings were to be found in the interior of the territory and not at the borders, just as we predicted. We conclude, therefore, that the two strategies of scent-marking shown by hyaenas are *not* species-specific but that they are responses to the problems of effectively marking areas of increasing size.

Number of occurences
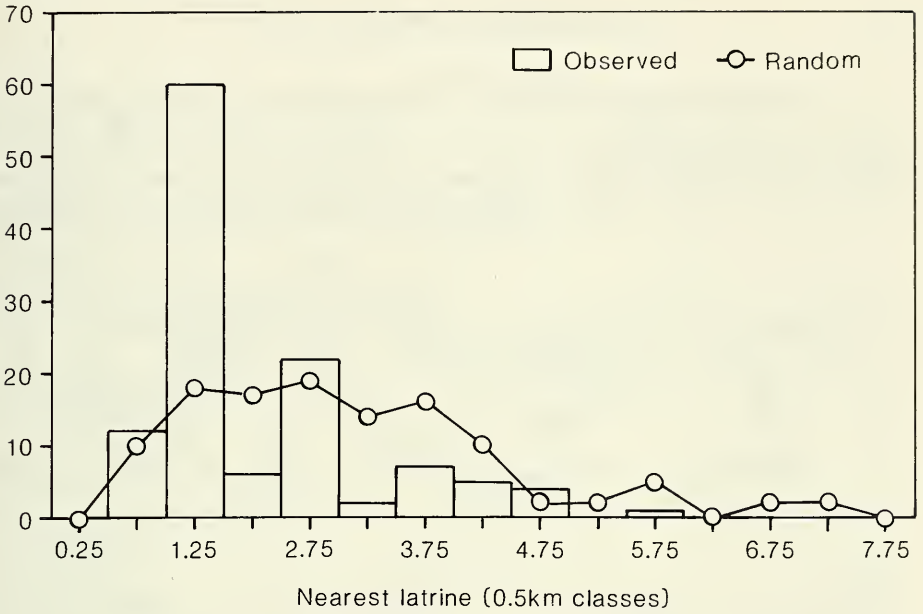
FIGURE 13.

The distribution of nearest neighbour distances for the latrines in the Kousant territory together with the random distribution. (After MILLS & GORMAN 1987).
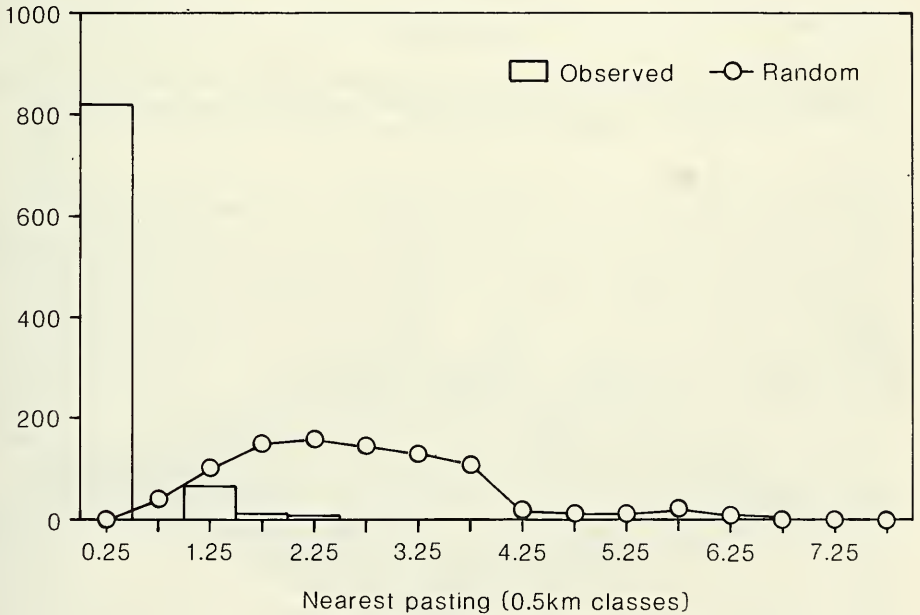
Number of occurences

FIGURE 14.

The distribution of nearest neighbour distances for the individual pastings (not pasting sites) in the Kousant territory, together with the random distribution. (After MILLS and GORMAN 1987).
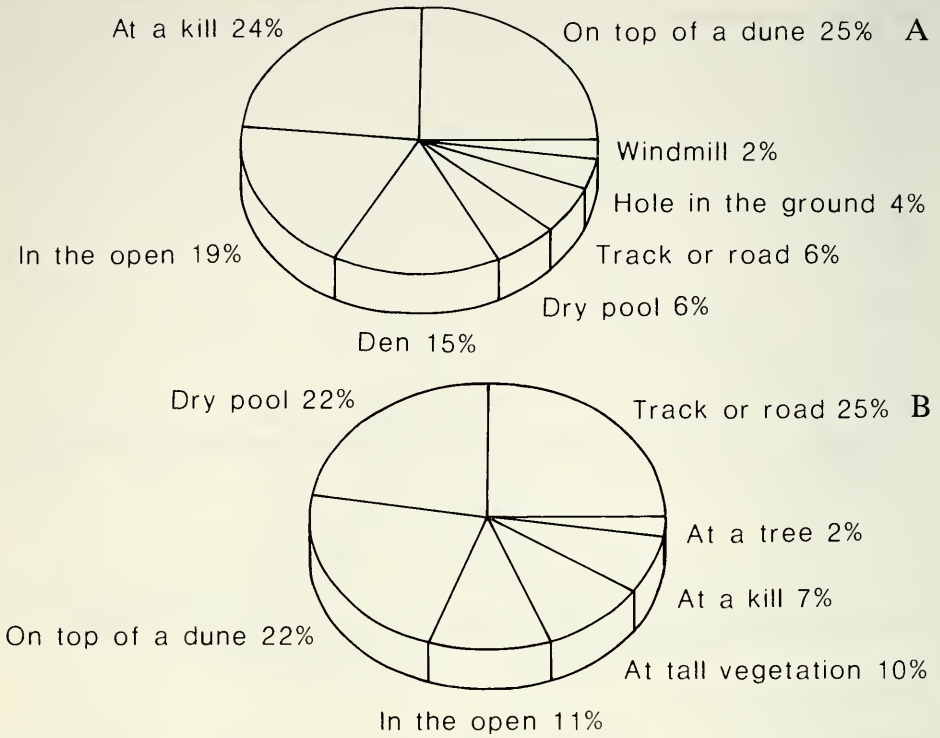
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FIGURE 15.

(a) The proportion of pastings, other than those deposited at latrines, associated with obvious environmental features. (b) The proportion of latrines associated with obvious landmarks. (After MILLS and GORMAN 1987).
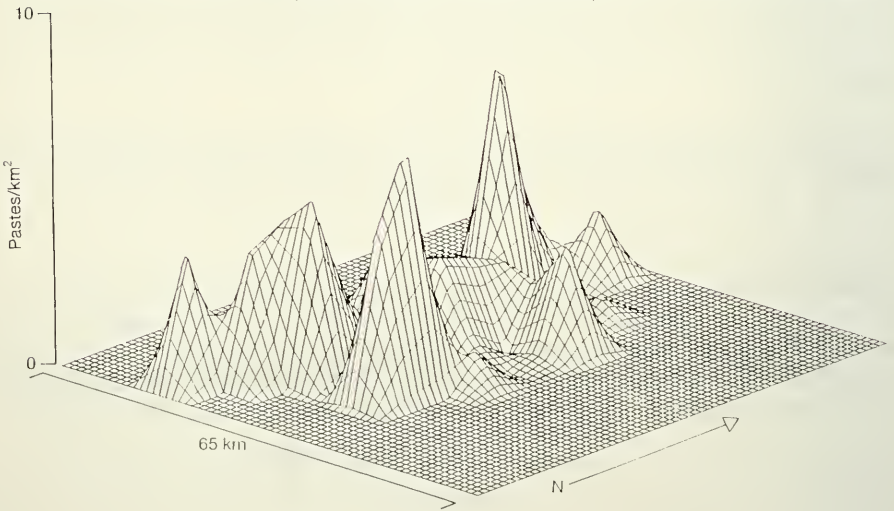

FIGURE 16.

A three dimensional map of the density of pastings in the Kousant group territory. Map parameters as in Figure 11.

THE EUROPEAN OTTER

In the British Isles the European otter lives not only in rivers and lakes, but also in the sea. Our studies on scent marking have been carried out on a marine population living around the Rhue peninsula in western Scotland (Fig. 17).
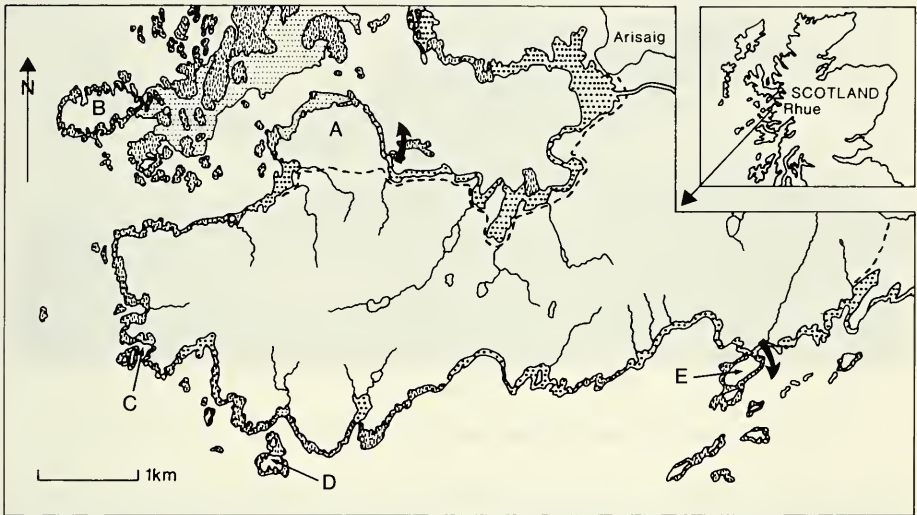

FIGURE 17.

A map of the Rhue peninsula in western Scotland.

European otters scent mark with spraints (faeces) which they place near nose height on the top of prominent objects such as large boulders or tussocks of grass throughout their home ranges or territories (Fig. 18). Repeated sprainting and urination at these sites by successive generations of otters can lead to the formation of distinct mounds and to the lush growth of nitrophilous algae and grasses which make the sites visually very conspicuous (Fig. 19). These sites we call *s p r a i n t   p i l e s* (GORMAN & TROWBRIDGE 1989). Our general approach has been to carefully map the precise positions of all of the spraint piles that are present along extensive stretches of the shoreline. We have then described their distribution by means of an analysis of nearest neighbour distances.

Around the Rhue peninsula, where otters forage almost exclusively in the sea, the spraint piles are arranged along the coast in an organised manner, with most being clumped together at distinct *s p r a i n t   s t a t i o n s* (TROWBRIDGE 1983). The clumped nature of the organisation can be clearly seen by comparing the frequency distribution of distances between spraint piles that would result were the same number to be dispersed randomly along the same stretch of coast (Fig. 20). Typically, a spraint station consists of a number of spraint piles connected one to the other, and to the sea, by distinct and well worn paths or trails through the vegetation (Fig. 21). The great

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FIGURE 18.

A European otter scent-marking with spraints. (Photograph courtesy of Jon Watt).

FIGURE 19.

Sprainting pile made by European otters on the west coast of Scotland. The mound, 42 cm high and grass covered, formed as a result of otters' sprainting at the same site for several generations. (Photograph courtesy of Beverley Trowbridge).
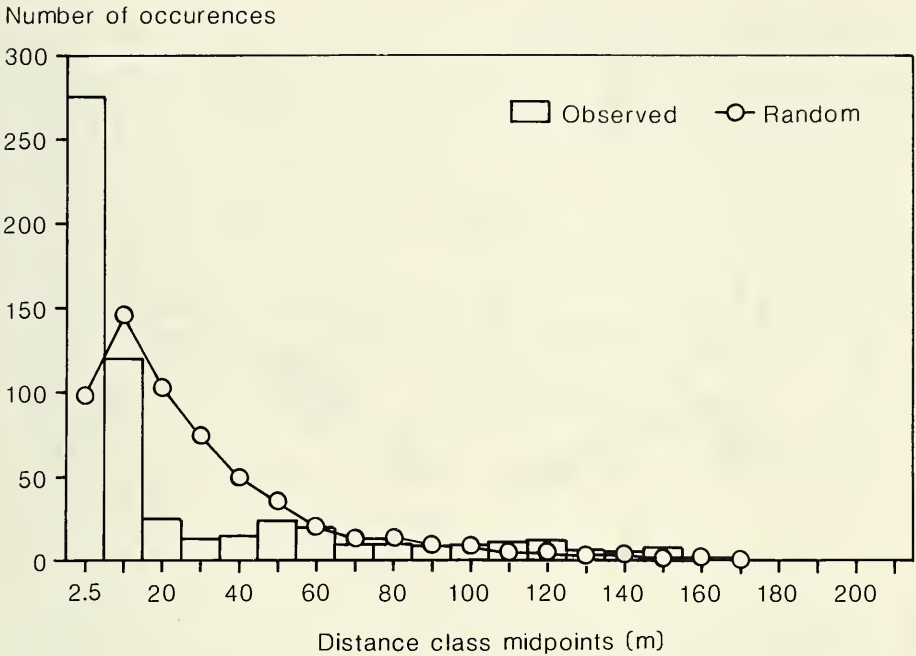
Number of occurences

FIGURE 20.

The frequency distribution of distances between spraint piles (n = 575) made by European otters on the Rhue peninsula. The expected distribution is that which would result were the same number of piles to be distributed at random around the 15.9 km peninsula and is the mean of 10 computer simulations. The two distributions are statistically different at p<0.001 (K-S test, D=0.3051). (After GORMAN & TROWBRIDGE 1989).

majority of spraint stations also contain a relatively large pool of freshwater. Within stations, nearly 50% of the spraint piles occur on the very edges of the freshwater pools, with the rest dispersed along the trails, many at junctions, thus ensuring their encounter whatever the direction of approach by an otter. The spraint stations are themselves distributed along the coast in a regular pattern, with a modal interstation distance of 50 m, and with very few stations closer together than 35 m or farther apart than 165 m (Fig. 22). The regular distribution of the spraint stations is not a consequence of the distribution of the freshwater pools which are essentially randomly dispersed along the coast (Fig. 23).

    With spraint stations spaced out in this way, at regular and frequent intervals along the coast, any otter landing from the sea will never be more than a short distance from the nearest scent marks and centre of information. Coastal otters require freshwater for drinking and, very importantly, for washing sea-salt from their fur. By placing their spraints on prominent objects, around and on the trails leading to freshwater pools, otters increase yet further the likelihood of them being detected by other individuals.
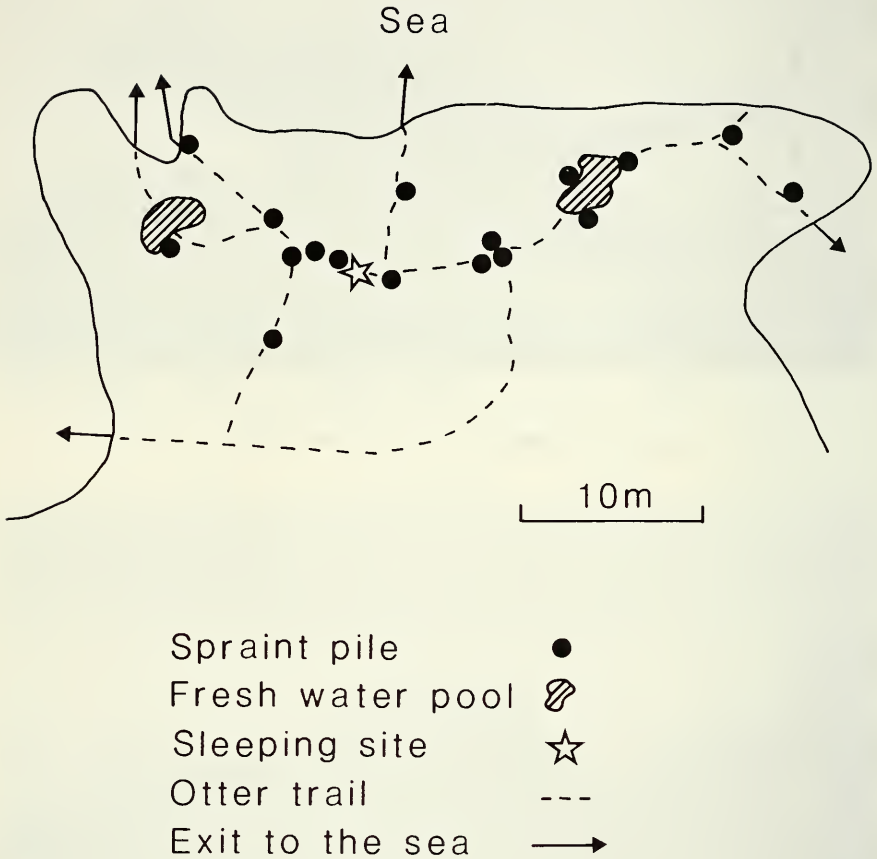
Sea

10m

Spraint pile   ●
Fresh water pool   ⬯
Sleeping site   ☆
Otter trail   - - -
Exit to the sea   ⟶

FIGURE 21.

A scale drawing of a spraint station showing the major environmental features.
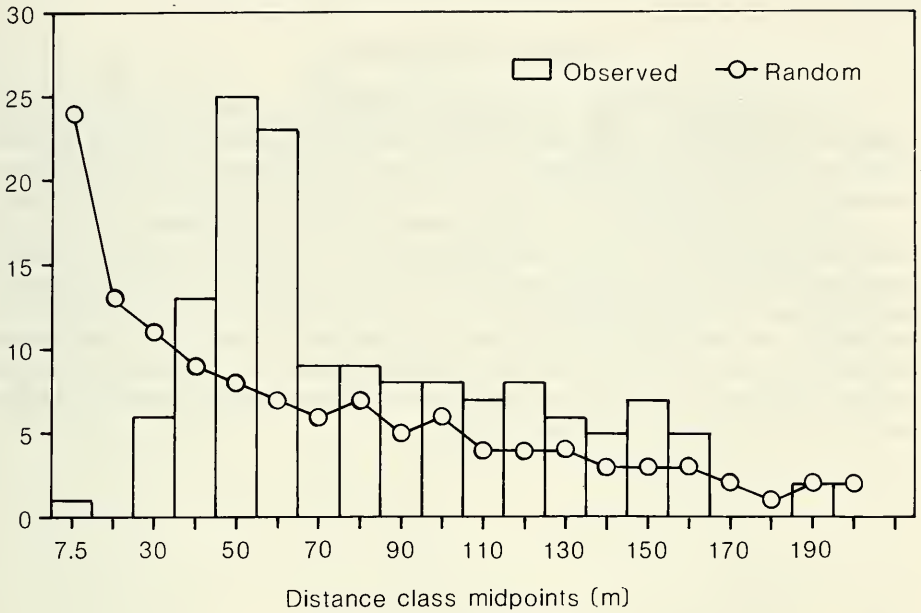(After GORMAN & TROWBRIDGE 1989).

Number of occurences

FIGURE 22.

The frequency distribution of distances between spraint stations (n = 143) on the Rhue peninsula. The expected, random distribution is the mean of 10 computer simulations and is significantly different from the observed distribution (K-S test, D = 0.2804; p < 0.001).
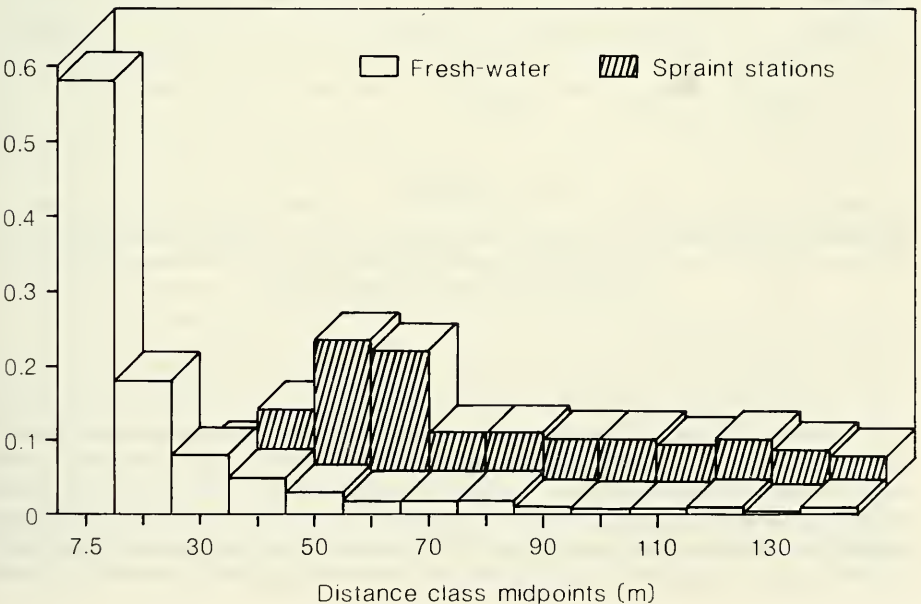(After GORMAN & TROWBRIDGE 1989).

FIGURE 23.

The frequency distribution of intervals between spraint stations compared to that between bodies of fresh water. The two distributions are significantly different at p < 0.001 (K-S test, D = 0.530.
(After Trowbridge, 1983).

THE EUROPEAN MOLE

The European mole is a fossorial insectivore that spends almost the whole of its life underground foraging in a system of permanent and semi-permanent tunnels. In the past it was very difficult to study this elusive creature, but now, with the aid of miniature radio-transmitters, it is possible to follow the movements of individual moles in some detail.

As befits their primitive nature, moles enjoy a relatively simple and straightforward social order. For most of the year established adults are solitary and sedentary creatures which occupy a mosaic of subterranean territories, rather like a deck of cards scattered on the ground (Fig. 24). The areas occupied by different individuals are largely exclusive and used by only one animal, although there is a small, varying degree of overlap between the ranges of some neighbours. Typically the ranges of males do not overlap with each other at all but each male range may overlap the ranges of a variable number of females and females may overlap with other females.
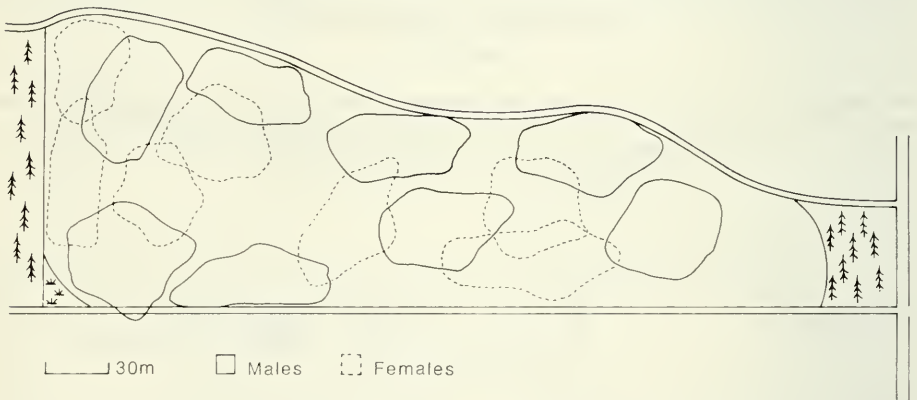

FIGURE 24.

The dispersion of territories in a population of European moles, as revealed by radio telemetry. The territories are depicted as the harmonic mean isopleth containing 95% of the radio fixes. (After data in Stone and Gorman 1985).

The apparent overlap between adjacent ranges involves mainly the interdigitation of tunnels in the soil column but there is also some sharing of communal tunnels. If two neighbours should meet in these jointly owned tunnels they will fight quite savagely. In reality, neighbours rarely meet in this way, but instead show a form of temporal avoidance with only one individual using the tunnels held in common at any one time and thus reduce the chances of overt aggression. Such avoidance behaviour was clearly shown by a group
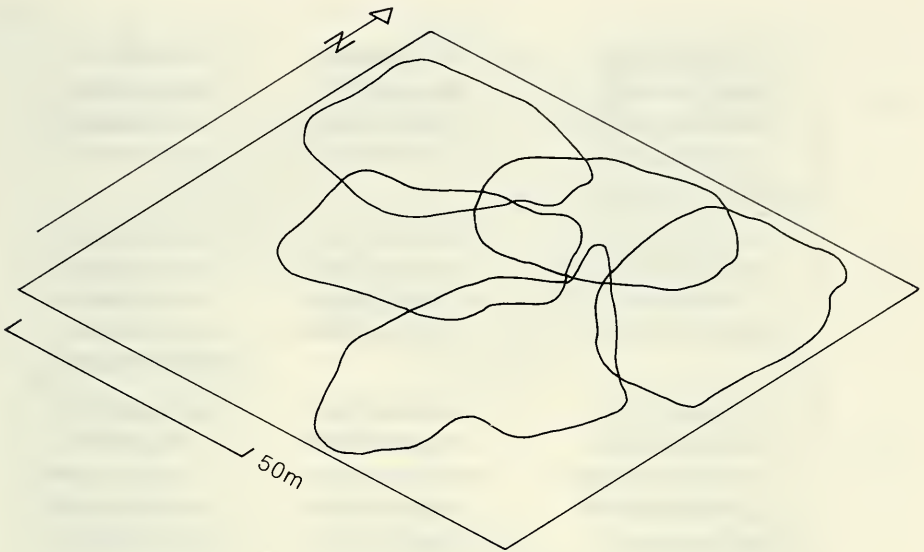
FIGURE 25.

The overlapping territories of five neighbouring moles.

of five neighbouring moles who were fitted with radio-transmitters and whose overlapping ranges and daily patterns of activity are shown in Figures 25 & 26. These five moles followed a typical pattern of activity with three periods of foraging per day, each alternating with a period of sleep spent in the nest. In addition, the activity of the moles was highly synchronised with all five leaving and returning to their nests at about the same time. Throughout the period that these animals were radio-tracked the area of overlap between the ranges of any two neighbours was exploited by only one individual during any given period of activity. This is clearly demonstrated in Figure 27 which shows the way in which all five moles exploited their ranges during three consecutive periods of activity. In these three dimensional maps the vertical dimension reflects the number of times an animal was located in different parts of its range. It is clear that although these animals were sharing areas of ground, and probably tunnels also, nevertheless they did so at different times of the day, and thus avoided meeting each other.

Apparently, moles are not only aware of the fact that an area of ground is occupied, but they also have sufficient awareness of the movement patterns of their neighbours to avoid meeting them in areas of range overlap. This implies that information is being passed, by one means or another, between individuals. Both male and female moles have a pair of preputial scent glands which open into the urethra and which add to the voided urine a secretion with an odour redolent of the general smell of a mole. We have shown elsewhere that moles will avoid the preputial secretions of other individuals (GORMAN and STONE 1989). There is the potential, therefore for moles to use urine to signal that an area is occupied and/or that a resident animal is currently active in a given area of tunnels. Mole ranges contain several hundreds of metres of tunnels and thus quite large quantities
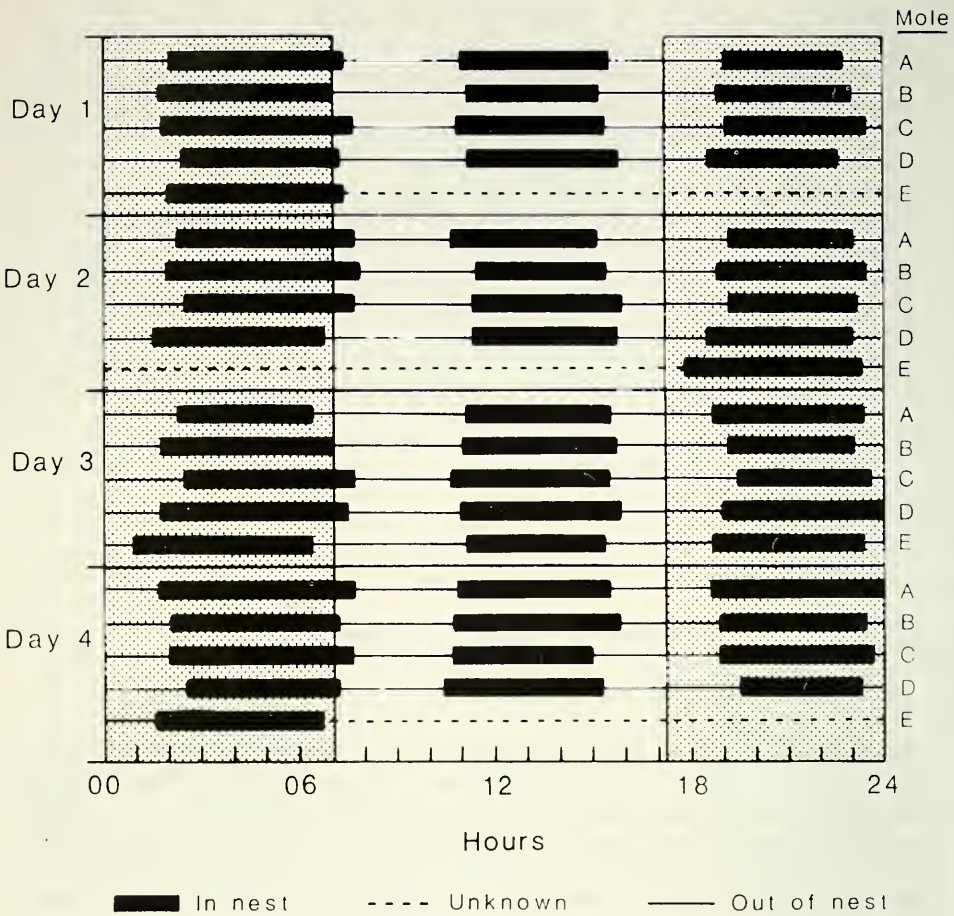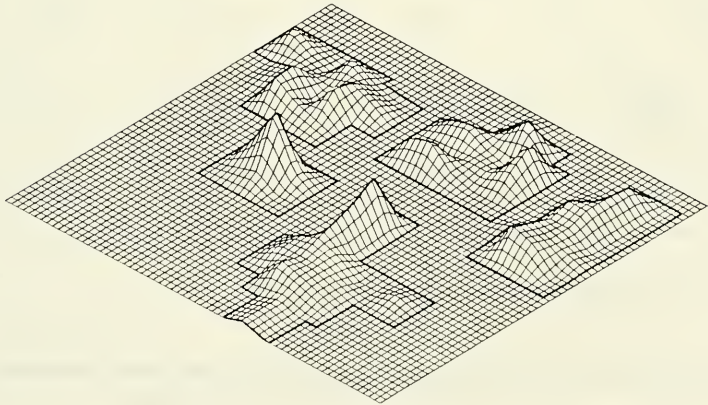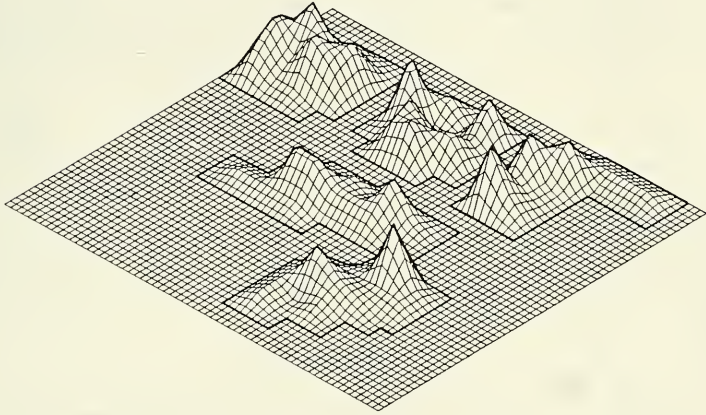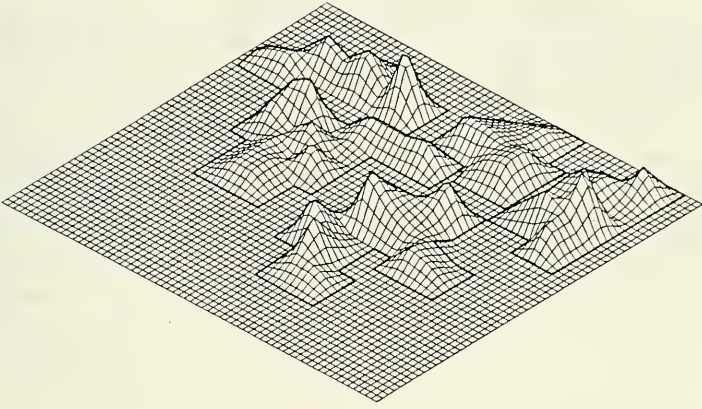
FIGURE 26.

The activity patterns of five neighbouring moles over a 4 day period. The stippled areas represent the hours of darkness.

FIGURE 27.

The areas used by each of the five moles during three consecutive activity periods. The plots were made by dividing the map into a matrix of 2.5 by 2.5 metre squares and counting the number of times the moles were located in each. The maps are drawn as if viewed from the south-east with the observation point situated 10,000 map units from the centre of the matrix and 200 above the horizontal.
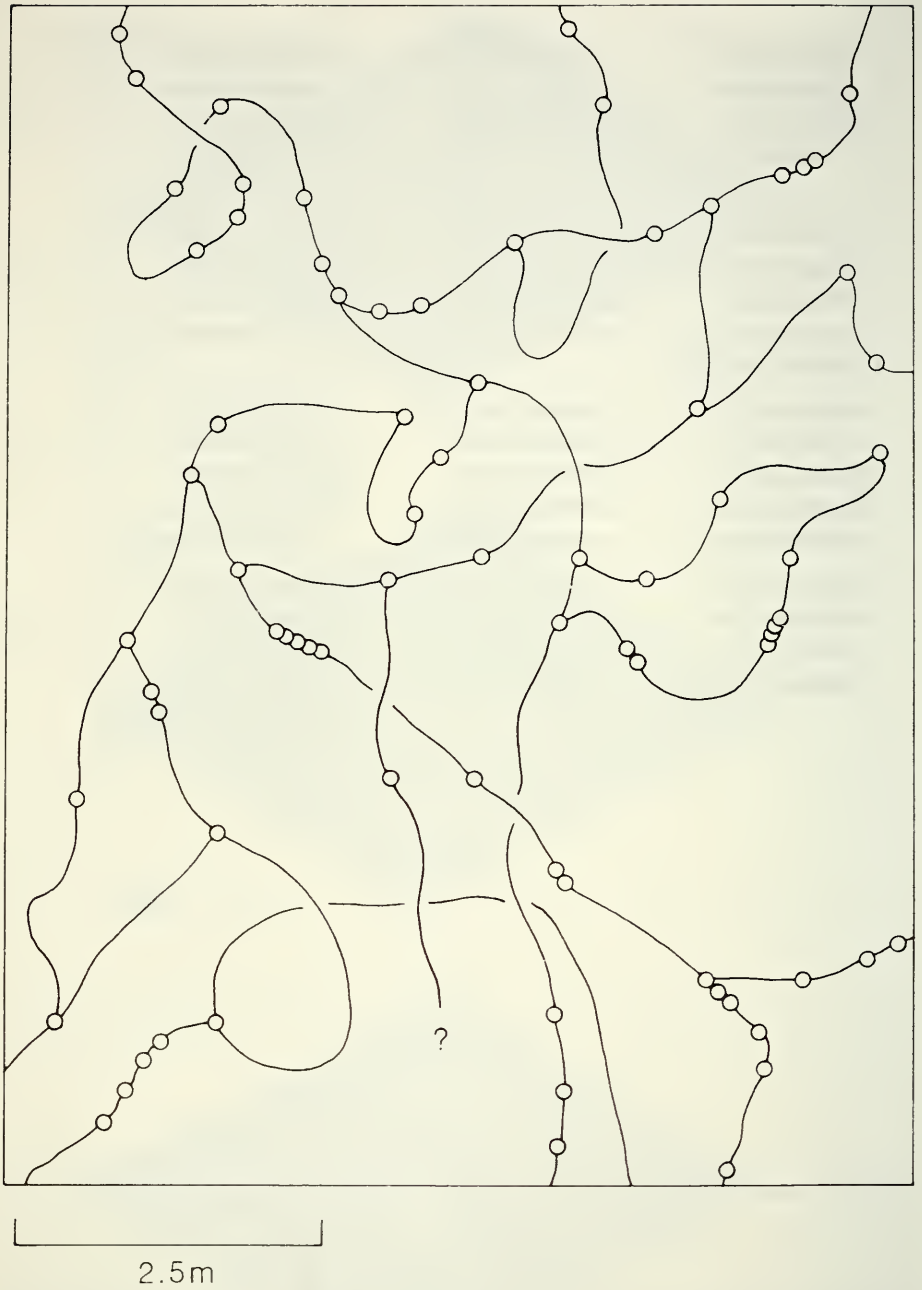
FIGURE 28.

An excavated area of the tunnel system of a European mole; the circles show where the mole had urinated in the previous 48 hours.

of urine will be required if the range is to be marked on the regular basis that seems to be required if neighbours are not to encroach. Thanks to the nature of their diet, moles do in fact produce copious quantities of urine; an average mole eats some 60 g of earth-worms each day, containing around 50 g of water. Given the high humidity of the tunnel system, most of this will be voided as urine.

Although urine is produced in large quantities it is, nevertheless a finite and limited resource. Once again, therefore, one would expect that if it is to be used for scent marking then moles will not urinate randomly, but instead in an organised pattern that maximises the chances of the urine being encountered by other moles. In order to see if this is indeed the case, we first of all determined, by radio-tracking, the extent of a male mole's range and the position of its tunnels. The animal was then recaptured and injected with a small quantity of ^{32}P, a radioactive isotope that is excreted in the urine. This accomplished, the mole was released back into its tunnel system for a further 48 h. A section of the mole's territory was then carefully excavated and all of the tunnels in the area were monitored for signs of radioactivity. All of the places where the level of radiation was at least 100% above background, and where there was no evidence of faecal material, are shown in Figure 28. As predicted, urine was deposited at distinct sites throughout the tunnel system; particularly noteworthy being the fact that all the tunnel junctions were marked in this way, thus maximising the chances of scent-marks being discovered by an intruding animal, regardless of its direction of travel.

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